

Egg Load Dynamics of *Homalodisca vitripennis*

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Environ. Entomol. 37(5): 1200–1207 (2008)

ABSTRACT *Homalodisca vitripennis*, the glassy-winged sharpshooter, poses a serious threat to grape production because of its ability to vector *Xylella fastidiosa*, the causal agent of Pierce's disease. The glassy-winged sharpshooter is native to the southeastern United States, and over the last 20 yr has expanded its range into Texas and California and more distantly into French Polynesia. A better understanding of the reproductive dynamics of *H. vitripennis* will aid in assessment of the invasiveness of this insect and may aid in refinement of control strategies. First, females of known age were dissected to determine egg maturation schedules. Females did not produce mature eggs until at least 1 wk after adult emergence. Oviposition reduced the number of mature eggs carried by females, suggesting a continuous cycle of egg deposition followed by egg maturation where females may experience transient egg limitation. Second, males and females were monitored over their entire lifetimes to determine longevity and fecundity. Males and females were long lived with an average lifespan of 4 mo. Females displayed one of three temporal patterns of oviposition: (1) no oviposition, (2) oviposition began <40 d after emergence, or (3) oviposition began >40 d after emergence. In general, oviposition was independent of female age. Finally, egg maturation rates of field-collected females were determined. Egg maturation rates varied with time of year and maximum egg maturation rates coincided with periods when oviposition was expected to be high. The highest egg maturation rate observed was five eggs per female per day.

KEY WORDS egg maturation, Pierce's disease, *Xylella fastidiosa*, invasive species

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae), was introduced to California during the late 1980s, most likely from the southeastern United States (Sorensen and Gill 1996). This insect poses a serious threat to California agriculture because of its ability to vector the bacterial pathogen, *Xylella fastidiosa* Wells et al. (Purcell et al. 1999, Almeida and Purcell 2003a, b). The bacterium, *X. fastidiosa*, is the causal agent of a wide range of plant diseases including Pierce's disease of grape, almond leaf scorch disease, citrus variegated chlorosis, and oleander leaf scorch (Hopkins and Purcell 2002). In California, losses caused by *H. vitripennis* have been a result of epidemics of oleander leaf scorch and Pierce's disease (Blua et al. 1999).

The glassy-winged sharpshooter is well established in southern portions of California, with discrete urban infestations in central portions of the state (CDFA 2008). To limit damage caused by this insect and its spread through the state, an intensive area-wide control program has been implemented to suppress glassy-winged sharpshooter populations in agricul-

tural and urban regions where it is currently established (Wendel et al. 2002, Hix et al. 2003, Toscano et al. 2004, Stone-Smith et al. 2005). In conjunction, a quarantine program, through disinfestation of nursery stock shipments, has been implemented to prevent movement of the glassy-winged sharpshooter to uninfested portions of California (Grafton-Cardwell et al. 2003a, b). Concerns of a *H. vitripennis* range expansion are not limited to California but are worldwide. The glassy-winged sharpshooter recently became established in the Pacific islands (French Polynesia, Hawaii, Easter Island; Grandgirard et al. 2006), and climate modeling indicates that portions of the wine grape-growing regions of Argentina, New Zealand, Australia, France, Spain, and Italy have climates that may be suitable for this insect (Peterson et al. 2003, Hoddle 2004).

An organism's reproductive potential is one of several factors that will affect the probability that a founding group of invaders can establish a viable population (Crawley 1986, Lawton and Brown 1986, Sakai et al. 2001). Similarly, reproductive potential will influence the speed with which a suppressed population can recover after an area-wide management tactic has been applied. Thus, a detailed understanding of *H. vitripennis* egg load dynamics will (1) aid in assessing the risk that an introduction would result in a viable population, (2) help determine the time required for

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populations to recover in the wake of an area-wide treatment, and (3) provide parameter estimates for population dynamics models. Recent studies have increased our knowledge of qualitative changes in glassy-winged sharpshooter reproductive phenology (Hummel et al. 2006a, b). Here I report on studies focused on quantifying the rate of *H. vitripennis* egg maturation and lifetime fecundity.

Materials and Methods

Field Site and Insect Collection. *Homalodisca vitripennis* adults and nymphs were collected from urban Bakersfield (Kern County, CA) in an area of mixed ornamental plantings dominated by Acacia (*Acacia redolens*), red-tipped photinia (*Photinia fraseri*), oleander (*Nerium oleander*), and crape myrtle (*Lagerstroemia indica*). Adults and nymphs were collected by beating foliage and allowing insects and nymphs to fall into a 40-cm-diameter sweep net. Insects were transported back to the laboratory in screened cages where they were sorted.

Plants and Cages. Three- to 6-wk-old cowpea, *Vigna unguiculata* cultivar black eye (Vermont Bean Seed, Randolph, WI), was used in all laboratory experiments. Plants were grown in 0.5-liter pots using Sunshine Soil Mix 1 (Sun Gro Horticulture, Bellevue, WA) and fertilized at planting with 2.5 ml of Osmocote 14-14-14 slow-release fertilizer (Scotts, Marysville, OH). Plants were staked to provide structural support. To cage insects on individual plants, 18.9 liter paint strainers (Louis M. Gerson Co., Middleboro, MA) were placed over each plant and sealed around the base of the pot. Plants used in experiments were replaced every 2–4 wk as needed to maintain uniform plant quality.

Grape, *Vitis vinefera* cultivar Chardonnay, also was used in one experiment. Grapes were grown in 1.3-liter pots using Sunshine Soil Mix 1 and fertilized once every 2 wk with 50 ml per pot of Sunshine Technigro 17-5-24 water soluble fertilizer (Sun Gro Horticulture). Insects were caged on individual grape plants using the same 18.9-liter paint strainers as used with cowpea. Plants and insects were maintained under 14:10 photoperiod and were held at ambient temperature, which cycled from a high $\approx 32^{\circ}\text{C}$ at mid-afternoon to a low of $\approx 18^{\circ}\text{C}$ at night.

Dissection of Females of Known Age. Late-instar nymphs were collected from the field and caged in groups of 5–10 per cowpea plant and monitored daily for adult emergence. On emergence, each newly eclosed female was paired with a single newly eclosed male and caged on a single cowpea. Each male-female pair was assigned to one of six treatments, which represented the time period over which females were allowed to mature eggs and oviposit before dissection. The treatments were 0, 4, 7, 14, 21, and 28 d posteclosion, with 18, 16, 8, 19, 18, and 19 male-female pairs per treatment, respectively. Insects were monitored over the prescribed period for oviposition and adult mortality. At the end of the prescribed period, females were frozen and dissected to determine the number of

mature eggs carried using methods adapted from those developed for parasitoids (Jervis and Copland 1996, Sisterson and Averill 2002). Eggs were considered mature provided they were similar in size, shape, and color to eggs deposited in egg masses.

For clarity, I define three terms which will be used throughout our analyses. First, I define “eggs carried” as the number of mature eggs carried by a female at the time of dissection. Second, I define “eggs deposited” as the number of eggs oviposited during the course of a test. Finally, I define “total egg load” as the sum of “eggs carried” and “eggs deposited,” which represents total potential reproductive output of a female over the study period. Analysis of variance (ANOVA) was used to compare number of eggs carried by females, number of eggs deposited, and total egg load (eggs carried + eggs deposited) on each dissection date. Data were log transformed before analysis. In addition, the relationship between number of eggs carried by females and number of eggs deposited by females with at least one mature egg on each dissection date was evaluated using linear regression (SAS Institute 2001).

Lifetime Fecundity in Laboratory. Similar to the experiments above, late-instar nymphs were collected from the field and held in groups of 5–10 per cowpea plant and monitored daily for adult emergence. On emergence, two newly eclosed females and two newly eclosed males were caged together on a single grape plant. Two sets of grape plants were used: grape that was inoculated ≈ 10 wk previously with the M23 strain of *X. fastidiosa* (Chen et al. 2005, 2007) and mock (i.e., water)-inoculated grape. Fifteen replicates per treatment were set up, resulting in a total of 60 male-female pairs (15 replicates per treatment \times 2 treatments \times 2 male-female pairs per treatment = 60). After 8 d on grape, insects were transferred to cowpea. The two males and two females on each grape plant were split so that each cowpea received a single male-female pair. Insects were monitored biweekly for oviposition and adult mortality over their entire lifespan. Cumulative fecundity and longevity was compared among females based on age of first oviposition using ANOVA (SAS Institute 2001).

Analysis of grape plants inoculated with *X. fastidiosa* using standard polymerase chain reaction (PCR) methods (Minsavage et al. 1994) subsequent to our tests indicated that all inoculations were unsuccessful. Thus, results from pairs originating from *X. fastidiosa* inoculated grape and mock-inoculated grape were pooled. This pooling was further justified because preliminary analyses of all measures presented here indicated no significant differences between insects held on the two grape types. Finally, adults that died before being transferred to cowpea were excluded from our analyses because all mortality on grape was caused by adults trapped in netting (i.e., paint strainers).

Egg Maturation of Field-Collected Females. The number of eggs matured per female per day in field populations throughout the year was estimated by comparing mean number of eggs carried by females on

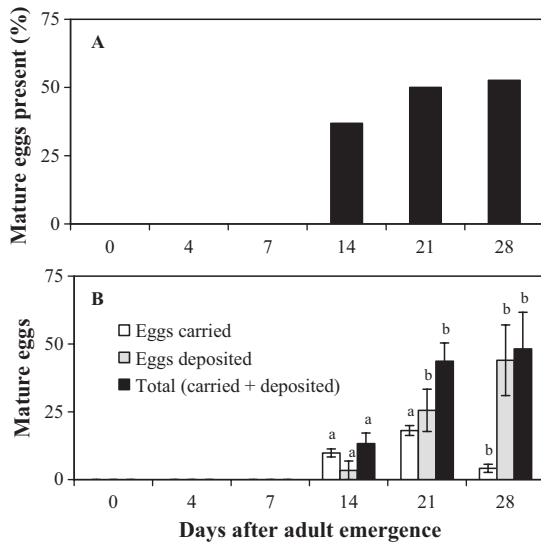


Fig. 1. Results of tests with fixed dissection dates. (A) Percent of dissected females with at least one mature egg. (B) The mean (\pm SE) number of eggs carried by females, number deposited, and total egg load (carried + deposited). Within categories (i.e., egg carried, eggs deposited, and total) and across dates, bars with different letters above them indicate significant differences.

the day of field collection to total egg loads of field-collected females provided a 1-wk oviposition period in the laboratory. Adult females were collected from the field on regular intervals between 2006 June and 2007 October. Sample sizes and amount of time between sample collections varied because of changes in field population levels of glassy-winged sharpshooter throughout the year. Thus, samples were less frequent and sample sizes were smaller in early spring than in midsummer. Samples were not collected during the winter when glassy-winged sharpshooter females were expected to be in reproductive diapause.

On return to the laboratory, females were randomly assigned to one of two groups. The first group was immediately frozen and dissected to estimate average number of eggs carried by females on arrival to the laboratory. Females in the second group were caged individually on cowpea for 1 wk. At the end of 1 wk, the number of eggs deposited was determined, and females were dissected to determine the number of eggs carried. Total egg loads for each female were determined by summing the number of eggs deposited over 1 wk and the mean number of eggs carried at the end of that week. Finally, for each sampling date, mean number of eggs matured per female per day was calculated by subtracting the mean number of eggs carried by females on arrival to the laboratory from the mean total egg load of females given a 1-wk oviposition period and dividing by seven.

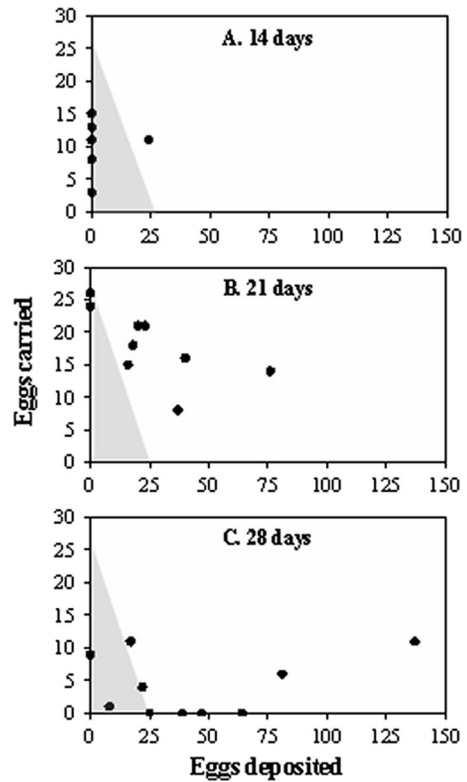


Fig. 2. Relationship of the number of eggs deposited with the number of eggs carried for females dissected 14 (A), 21 (B), and 28 (C) d after eclosion. The shaded area indicates the region where total egg loads are <25 .

Results

Egg Maturation in Laboratory. No mature eggs were deposited or present in dissected females until 14 d after eclosion (Fig. 1A). Approximately 50% of females dissected 14, 21, and 28 d posteclosion carried or deposited at least one mature egg (Fig. 1A). In analyses that excluded females that produced no mature eggs, there was a significant effect of dissection date on the number of eggs carried by females ($F = 19.6$; $df = 2,23$; $P < 0.0001$), number of eggs deposited ($F = 3.9$; $df = 2,23$; $P = 0.035$), and a marginally significant effect on total egg load ($F = 3.2$; $df = 2,23$; $P = 0.06$; Fig. 1B).

The relationship between number of eggs deposited and number of eggs carried was not significant on day 14 ($F = 0.08$; $df = 1,5$; $P = 0.78$; Fig. 2A) or day 28 ($F = 0.51$; $df = 1,8$; $P = 0.49$; Fig. 2C), but on day 21 there was a significant negative association between number of eggs deposited and number of eggs carried ($F = 5.77$; $df = 1,7$; $P = 0.047$; Fig. 2B). Analysis of these relationships suggests two characteristics about *H. vitripennis* egg load dynamics. First, it seems that females do not initiate oviposition until a minimum number of eggs matured. Ninety-four percent of females that had oviposited after 14, 21, or 28 d had a total egg load ≥ 25 , whereas 88% of females that did not oviposit had an

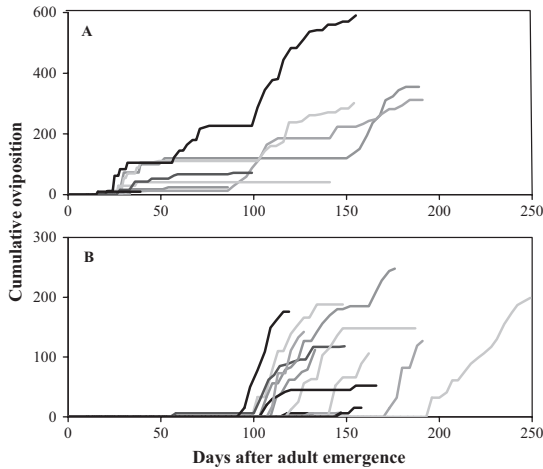


Fig. 3. Cumulative oviposition curves for (A) females that oviposited within 40 d of eclosion and (B) females that oviposited for the first time > 40 d after eclosion. Each line represents results for a single female.

egg load <25 eggs (Fig. 2). From the data presented here, this threshold seems to be ≈ 25 eggs. Second, mature eggs seem to be deposited faster than new eggs are matured. This is evidenced by a lack of a significant increase in total egg load between days 21 and 28 (Fig. 1B), but a significant decrease in the number of eggs carried by females between days 21 and 28 (Fig. 1B).

Lifetime Fecundity in Laboratory. Three patterns of lifetime oviposition were observed: (1) females never oviposited, (2) females began ovipositing <40 d after eclosion, or (3) females began ovipositing >40 d after eclosion. Forty-four percent of females never oviposited, despite an average (\pm SD) lifespan of 107 ± 42 d. Nineteen percent oviposited for the first time within 40 d of eclosion, with a mean date of first oviposition of 25.6 ± 5.7 d posteclosion (Fig. 3A). Finally, 37% oviposited for the first time >40 d after eclosion with a mean date of first oviposition of 124.4 ± 33.5 d (Fig. 3B). Females that oviposited eggs before 40 d deposited numerically more eggs than females that began ovipositing after 40 d (mean \pm SD: 213.3 ± 209.2 versus 110.1 ± 77.8 ; Fig. 3), although this effect was not significant ($F = 0.61$; $df = 1,21$; $P = 0.44$). Females in both groups showed frequent breaks in oviposition, and the longest break in oviposition was 99 d.

Females that laid eggs before 40 d had a shorter lifespan than females that began ovipositing after 40 d (mean \pm SD: 131.8 ± 53.0 versus 159.4 ± 32.5 d), but this effect was not significant ($F = 2.43$; $df = 1,21$; $P = 0.13$). Across all groups and sexes, adult life spans on cowpea were long (mean \pm SE: 121.5 ± 4.9 d), and the longest observed life span was 249 d (Fig. 4). Male and female survival was similar, although females had a marginally significantly longer mean lifespan (mean \pm SE: males, 113.6 ± 6.6 ; females, 131.1 ± 7.3 ; $t = 1.78$; $df = 89$; $P = 0.08$; Fig. 4). Survivorship curves for males and females were between type I and type II. This

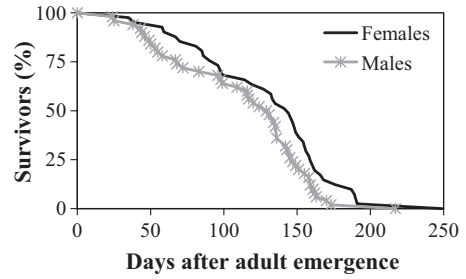


Fig. 4. Survival curves for males and females.

seems reasonable because most mortality was from natural causes, although some mortality was likely caused by forces that would act independent of age such as getting caught in netting.

Egg Maturation of Field-Collected Females. The mean number of eggs carried by females on arrival to the laboratory and total egg loads of females after a 1-wk oviposition period varied by collection date (Fig. 5A and B). There were two peaks in total egg load of

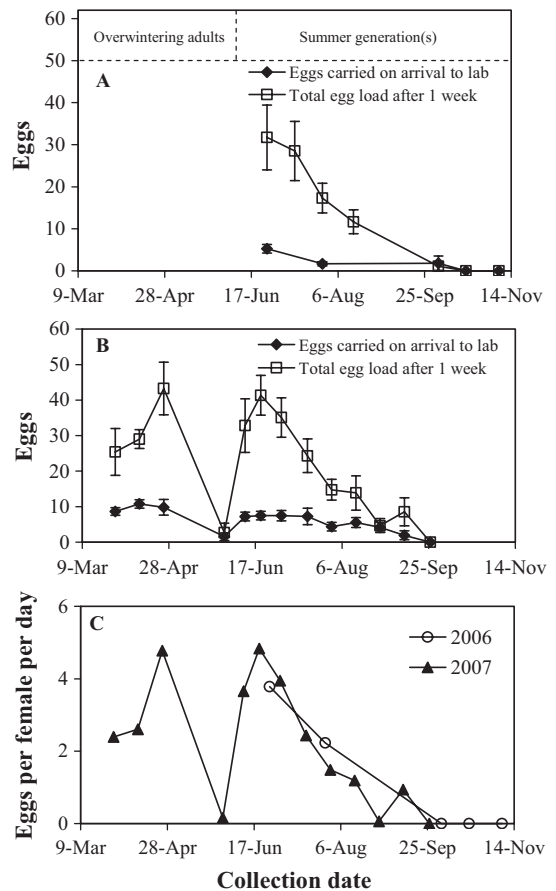


Fig. 5. Eggs carried and egg loads after a 1-wk oviposition period for females collected in 2006 (A) and 2007 (B). (C) Estimated egg maturation rates (eggs per female per day) of field-collected females.

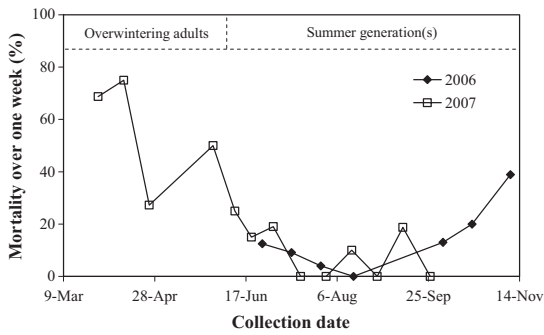


Fig. 6. Mortality of field-collected females provided a 1-wk oviposition period.

females provided a 1-wk oviposition period. The first occurred in late April, during the period when overwintering females were ovipositing. The second occurred in mid-June, shortly after emergence of the first generation of adults. There was considerably more variation in total egg loads of females given a 1-wk oviposition period than in the number of eggs carried by females on arrival to the laboratory (Fig. 5A and B).

The highest rates of egg maturation coincided with peaks in total egg load of females provided a 1-wk oviposition period, with ≈ 5 eggs matured per female per day (Fig. 5C). Egg maturation rates declined after each peak and females matured few eggs between the end of the overwintering oviposition period and emergence of first-generation adults and after late October (Fig. 5C). Mortality of adults collected from the overwintering generation was high (28 March to 20 May), and the greatest rate of egg maturation observed in overwintering adults occurred in the collection with the lowest mortality (cf. Figs. 6 and 5B). Mortality of field-collected adults through the summer was low and increased again in the fall (Fig. 6).

Discussion

Females did not produce mature eggs until >7 d posteclosion (Fig. 1), a time scale similar to the 9.4-d preoviposition period reported by Sétamou and Jones (2005). In tests with fixed dissection dates, 96% of ovipositing females had egg loads ≥ 25 eggs (Fig. 2) and for 21-d-old females, there was a negative relationship between number of eggs deposited and number of eggs carried by females (Fig. 2B). These observations suggest that females typically do not oviposit until a minimum number of eggs are matured and that mature eggs are deposited faster than new eggs are matured. The rate at which females from field populations matured eggs varied with time of year and the number of eggs carried by females on arrival to the laboratory was typically low (Fig. 5). Finally, frequent breaks in oviposition of laboratory reared females were observed (Fig. 3).

In experiments with fixed dissection date, only 52% of females matured eggs by 28 d (Fig. 1A). Similarly, in females monitored over their entire lifespan, 44%

never oviposited, and of those that oviposited, 66% did not oviposit until >40 d posteclosion (Fig. 3B). These results, which used adults reared from field-collected nymphs, differ from those of Sétamou and Jones (2005), who used adults from a laboratory colony. In their study, 88% of females oviposited. It is not clear why some females in our tests never matured eggs or showed long delays before egg laying was initiated. Because plant quality and environmental conditions were similar for all insects, these factors are unlikely to be responsible. One hypothesis is that mating may have influenced timing of egg maturation and/or oviposition in our tests. In lifetime fecundity tests, 27% (4 of 15 females) of females that did not oviposit until 40 d posteclosion and 25% (2 of 8 females) of females that oviposited within 40 d of eclosion were observed mating a week before their first oviposition. In contrast, females that never oviposited were never observed mating. These observations suggest that timing of mating may have influenced timing of first oviposition.

Egg maturation dynamics are particularly well studied in holometabolous insects in the orders Lepidoptera and Hymenoptera (Boggs 1997, Jervis et al. 2001, 2005, 2007, Jervis and Ferns 2004), but studies with hemimetabolous insects are limited. The standard approach with Hymenoptera and Lepidoptera is to describe timing of egg maturation relative to emergence of the adult female. Species with females that emerge with their full complement of mature eggs are considered pro-ovigenic, whereas species with females that do not are considered synovigenic (i.e., egg production and maturation occurs throughout their lives; Jervis et al. 2001). Similarly, the proportion of the lifetime complement of eggs that are mature on emergence of the adult female is calculated and referred to as the "ovigeny-index" (Jervis and Ferns 2004, Jervis et al. 2001, 2007). As female *H. vitripennis* emerge without mature eggs, they can be considered synovigenic with an ovigeny-index of 0. This condition may be common for members of the family Cicadellidae, because a preoviposition period of several days is commonly observed in this group (Nielson 1968, Nielson and Toles 1968, Hoffman et al. 1991, Duan and Messing 2000, Tokuda and Matsumura 2005). Within the phytophagous Hemiptera, however, there is likely to be some variations in ovigeny-index because at least one species of Aleyrodidae emerges with a portion of its egg complement matured (Coombs et al. 2007).

Within Lepidoptera and Hymenoptera, a low ovigeny-index is associated with two life history characteristics. First, a low ovigeny-index suggests that juvenile resources are less important for egg production than adult resources (Jervis et al. 2005). Second, across species, there is a negative association of ovigeny-index with lifespan (Jervis et al. 2001, 2005). Thus, insects with longer life spans tend to have low ovigeny-indices. The data collected here support the contention that adult resources are more important in egg production than juvenile resources. Specifically, dissection of field-collected females immediately on return to the laboratory indicates that the number of eggs carried by field collected females is typically low

(Fig. 5A and B), indicating that adult resources are required to mature additional eggs. Because the latter prediction is across species, fully assessing the prediction of a negative association of ovigeny-index with lifespan is not possible, because ovigeny-index values have not been estimated for other phytophagous Hemipterans. Nonetheless, *H. vitripennis* has a low ovigeny-index and a very long lifespan in the laboratory (Fig. 4), conforming to this prediction.

For insects that mature eggs continuously as adults, the greatest constraint on reproduction is the rate at which eggs are matured. If the rate at which eggs are matured is less than the rate at which acceptable hosts are encountered, females are likely to experience transient egg limitation (i.e., periods during which high quality hosts are encountered but for which females lack eggs to deposit; Rosenheim et al. 2000). In tests with field-collected females, I found that females matured a maximum of 5 eggs/d and that the number of eggs carried by females on arrival to the laboratory from the field was typically low (Fig. 5). Because ovipositional sites for this polyphagous insect are abundant, my data suggest that reproductive rates in the field may indeed be constrained by egg maturation rates. Consequently, factors that influence *H. vitripennis* egg maturation rates are likely to effect population growth rates.

It is reasonable to hypothesize that the choice of feeding/ovipositional host may affect egg maturation rates and that female host choice may be driven by the nutritional requirements for egg maturation. There is some evidence for both aspects of this hypothesis. First, on a single date (28 July 2006), I compared egg maturation rates of insects held on cowpea versus sorghum. In this test, females on cowpea matured eggs at a rate of 2.2 per female per day (Fig. 5A; 28 July 2006), whereas on sorghum, the daily egg maturation rate was 0.30 per female per day ($t = 3.7$; $df = 26$; $P < 0.01$). In terms of the second aspect, Brodbeck et al. (2007) compared adult host preference to nymphal performance on the same hosts and found that the two were not correlated. Brodbeck et al. (2007) concluded that adult preference was driven by suitability of the host for adult resources and not for their offspring. This evidence suggests there is some credence to the above hypothesis, although further investigation into the dynamic role of host choice with reproductive rate is needed.

Knowledge of the age of first reproduction and how reproduction changes over a female's lifetime aids in evaluating the risk posed by a single female on arrival to a currently uninfested area. For example, if oviposition declines with female age, the risk that a single female could establish a new population decreases with the age of that female. In contrast, if there is no relationship between female age and oviposition, female age will not impact risk of establishment. The results presented here indicate that adults are long lived (Fig. 4) and, in agreement with Sétamou and Jones (2005), there was no relationship between female age and number of eggs deposited (Fig. 3). Thus, for *H. vitripennis*, female age is unlikely to affect the

probability that a new population is established by a founding female. An additional factor to consider is timing of mating relative to emergence and the number of times a female must mate to fertilize their full complement of eggs. Dissection of field collected females from southern California indicates that mated females are present year round (Hummel et al. 2006a). Similarly, Hix (2001) observed that females typically mated a single time shortly after eclosion. Thus, it seems reasonable to presume that any single field-collected female has already mated and does not need to remate to oviposit fertilized eggs over their lifetime. Independence of oviposition from female age and the potential for females to require only a single mating shortly after eclosion perhaps explains partially why this insect has been successful at invading new areas.

Egg maturation rates of field-collected females varied with time of year (Fig. 5C). This was expected, because Hummel et al. (2006b) showed that the reproductive phenology of *H. vitripennis* populations changes over the course of the year. Two peaks in egg maturation rates were observed. The first occurred in spring (April) and coincided with the period during which overwintering females are expected to oviposit. The apparent increase in egg maturation rates from March to April (Fig. 5) may be an artifact because of high mortality of field-collected females in the laboratory during two of the three tests conducted over this period (Fig. 6). In addition, field observations indicated that a high number of eggs were deposited by the beginning of April because of the presence of a large number of first-instar nymphs at field sites. The second peak in egg maturation occurred in late spring/early summer (June) and coincided with emergence of the first summer generation (Fig. 5A and B). A third peak in egg maturation rate that would coincide with the emergence of the second summer generation was not observed. This may have occurred for two reasons. First, a flush of second-generation adults is typically not observed at our collection site, presumably because of high egg parasitism during the summer (Krugner 2007). Second, adults that emerge in late summer or early fall may be in reproductive diapause and thus would not carry mature eggs.

In conclusion, the results indicate that *H. vitripennis* females can produce a large number of eggs over their lifetime (>100 per female; Fig. 3) and have a long life span (Fig. 4). These life history characteristics combined with the polyphagous nature of this insect suggest that populations can grow rapidly and are unlikely to be limited by availability of suitable hosts. The population growth potential of this insect may be best exemplified by the increase in population size between the overwintering generation and the first summer generation. Specifically, adults are typically scarce during the winter, whereas the size of the first summer generation is typically large (Castle et al. 2005, Krugner 2007). Such ability to recover from bottle necks will make this insect difficult to suppress over the long term without continued monitoring and treatment.

Acknowledgments

I thank S. Uchima and D. Dwyer for technical assistance. N. Hummel, R. Krugner, and D. Stenger provided helpful comments on an earlier draft of this manuscript. This article is in the public domain and not copyrightable. It may be freely reprinted with customary crediting of source.

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Received 24 March 2008; accepted 9 July 2008.